

STREPTOPUS OREOPOLUS FERN., A HYBRID TAXON

DORIS LÖVE AND HINRICH HARRIES

In 1905, M. L. Fernald and J. F. Collins visited Mt. Albert on the Gaspé Peninsula in eastern Quebec. Above timberline they discovered on this mountain a remarkable *Streptopus* with deep claret-colored flowers. This plant proved to be a new taxon and was named by Fernald (1906) *Streptopus oreopolus*, the mountain-dwelling twisted-stalk.

Next summer, when Fernald and Collins botanized again in the mountains of the Gaspé, doubts entered Fernald's mind and he suggested (Fernald, 1907) that the new species might be a hybrid between *S. amplexifolius* (L.) DC. and *S. roseus* Michx. This hypothesis appeared to be supported by Fernald's observation that the fruits of *S. oreopolus* did not develop to maturity, though he considered also the possibility that the extremely dry weather during the early part of this particular summer might have been responsible for the sterile condition. There were also certain features of the plant and its occurrence which made Fernald hesitant in proposing his hypothesis (p. 107): "This uniform sterility of *S. oreopolus* throughout its known range suggests that it may not be a self-perpetuating species; yet, if this should prove to be the case, the profusion of the plant throughout the area and the constancy with which it maintains its characteristic pubescence and the color of its perianth is indeed remarkable."

In 1929, a review of the literature on *S. oreopolus* and a discussion of its taxonomic position and distribution were given by Marie-Victorin in his work on "les Liliiflores du Québec". By this time the taxon had been reported from northwestern Newfoundland (Fernald, 1926), the Mingan Archipelago (Marie-Victorin, 1929), the Shickshock Mountains (Fernald, 1906, 1907), Mt. Katahdin (Stebbins, 1929), and Mt. Washington (Fernald, 1927), and plants with apparently well-developed fruits had been found on two occasions (Fernald, 1926; Marie-Victorin, 1929). Marie-Victorin rejected the possibility of a hybrid origin for *S.*

oreopolus especially because of the dark red color of its flowers which he thought could not be the result of a hybridization between two parent species with respectively white and rose-colored flowers. Instead, he considered the taxon to be a good species which he classified (p. 98) "dans la catégorie des endémiques de la région non récemment glaciée qui entoure le golfe Saint-Laurent".

The taxonomic position of *S. oreopolus* was discussed again by Fassett (1935). From Fassett's description of the taxon, as from the previous paper by Marie-Victorin (1929), it is apparent that *S. oreopolus*, while intermediate between *S. amplexifolius* and *S. roseus* in certain vegetative features and in the character of the fruits, is much more similar to *S. amplexifolius*, especially with respect to the flowers. Fassett reached the conclusion that *S. oreopolus* is a mere variety of *S. amplexifolius* and closely related to the var. *denticulatus* which occurs in the Lake Superior area and in western North America. The latter variety, according to Fassett, approaches *S. oreopolus* in its denticulate leaf margins and in its occasionally pink or reddish flowers. Fassett agreed with Marie-Victorin in rejecting the possibility that *S. oreopolus* might be a hybrid. He reports as additional evidence against such an interpretation of the taxon his observation (p. 101), "that *S. oreopolus* has the perianth-segments conspicuously papillate within, while *S. amplexifolius* var. *americanus* rarely has well-developed papillae, and the representative of *S. roseus* occurring in that region lacks papillae of the type found in the purported hybrid". The distribution of *S. oreopolus* appeared to Fassett to be likewise in disagreement with the hybrid hypothesis because (pp. 101-102), "if *S. amplexifolius* and *S. roseus* can hybridize, why do they not do so in the many other places where their ranges overlap, instead of only in one limited region".

Fassett (*l.c.*) reported also the occurrence of a plant which appeared to be an intermediate or hybrid between *S. amplexifolius* and *S. oreopolus* (p. 102): "On Mount Washington, New Hampshire, just above Tuckerman's

Ravine, may be found a most interesting series of variations of *S. amplexifolius*. Var. *oreopolus* is abundant, and var. *americanus* can also be found. A third type of plant has denticulate leaves like those of var. *denticulatus*. Since its leaf-margin is intermediate between that of var. *americanus* and that of var. *oreopolus*, and, in addition, the lower leaf-surface is less glaucous than in the former, but more so than in the latter, it is considered as a hybrid of these two varieties. The flowers, which were just beginning to open when observed by the writer on June 27, 1934, were nearly white and conspicuously papillate within. . . . The expanded flowers should be observed, especially for correlation of perianth-color with degree of tooting on the leaf-margin, and the fruit-colors should be noted."

We ourselves have observed for several years the three kinds of *Streptopus* in the subalpine region of Mt. Washington. There, *S. amplexifolius* is represented by its var. *americanus* Schultes and *S. roseus* by var. *perspectus* Fassett. *Streptopus oreopolus* has been collected at the Lakes of the Clouds (No. 7512, July 25, 1958, in deep moss around the Lakes at 5100' alt., coll. A. & D. Löve), along the Oakes Gulf Trail (No. 346, August 5, 1961, in subalpine birch-fir forest at 4300' alt., coll. H. Harries), in the upper part of the Tuckerman Ravine headwall (August 28, 1962, in the subalpine *Alnus*-shrubbery around the trail, fruits coll. by D. Löve), and on the east slope of Mt. Clay (No. 347, July 18, 1961, at 5350' alt., coll. H. Harries).

In the subalpine region of Mt. Washington, the three taxa occur mainly in sheltered locations on the northeast, east, and southeast slopes between 4500' and 5500' alt. where because of the thick and long-lasting snow cover the fir krummholz is replaced by a subalpine snowbed vegetation. In these localities, the three *Streptopus* forms grow associated with such snow-tolerant species as *Betula glandulosa*, *Vaccinium caespitosum*, *Calamagrostis canadensis* s.l., *Deschampsia flexuosa*, *Luzula parviflora* var. *melanocarpa*, *Veratrum viride*, *Clintonia borealis*, *Houstonia caerulea* var. *Faxonorum*, *Solidago macrophylla* var. *thyrsoides*, and

Dryopteris spinulosa var. *americana*. On such sites, the snow cover was observed in spring 1961 to disappear between May 20 and June 13. In a few spots where the snow cover lingered into late June or early July, *Streptopus* was found to be lacking.

In their subalpine localities, *S. amplexifolius* and *S. oreopolus* grow mostly in the furrows which are frequently met with in snow bed areas on steeper slopes, and generally along drainage channels. In the forests of the lower altitudes, *S. amplexifolius* was encountered occasionally, mostly in close vicinity to a stream. *S. oreopolus* was found in such a habitat only once, namely in Oakes Gulf at 4300' alt. where it was observed together with *S. amplexifolius* in a subalpine birch-fir forest along the margin of a small stream.

Streptopus roseus does not show such a pronounced preference for drainage channels but is of a more general distribution and is found even in some of the more luxurious kinds of heath vegetation. The species was noted by us in the Mt. Washington area only from subalpine localities and has not been observed in forest habitats, but it is cited by Pease (1924) for many low-altitude localities in the area.

Streptopus amplexifolius and *S. roseus* resemble each other in their wide altitudinal range which extends from the valley levels up into the subalpine region where both species reach their altitudinal boundary, according to our observations, between 5400' and 5500' alt. *Streptopus oreopolus*, on the other hand, was observed only between 4300' and 5400' alt. and appears to be a strictly subalpine taxon.

In the subalpine region of Mt. Washington, the three *Streptopus* taxa were found to flower between late June and early August. In 1961, the peak of the flowering fell for *S. amplexifolius* and *S. oreopolus* between July 10 and July 20; that of *S. roseus* was about a week earlier.

We noted in the subalpine region of Mt. Washington the color of the flower to be a good characteristic with all three taxa. The flowers of *S. amplexifolius* are creamy white with a dark purple streak at the base of each perianth lobe. The flowers of *S. roseus* are rose-colored with many irregularly

scattered darker red streaklets. The flowers of *S. oreopolus* lack any kind of markings. They are white in the bud and become dark wine red at maturity (appearing almost black in herbarium specimens).

We now have chromosome counts of all three taxa from the Mt. Washington area. *Streptopus roseus* is diploid ($2n=16$, counted by Dr. S. Kawano on material collected at the Lakes of the Clouds in July, 1960). *Streptopus oreopolus* is

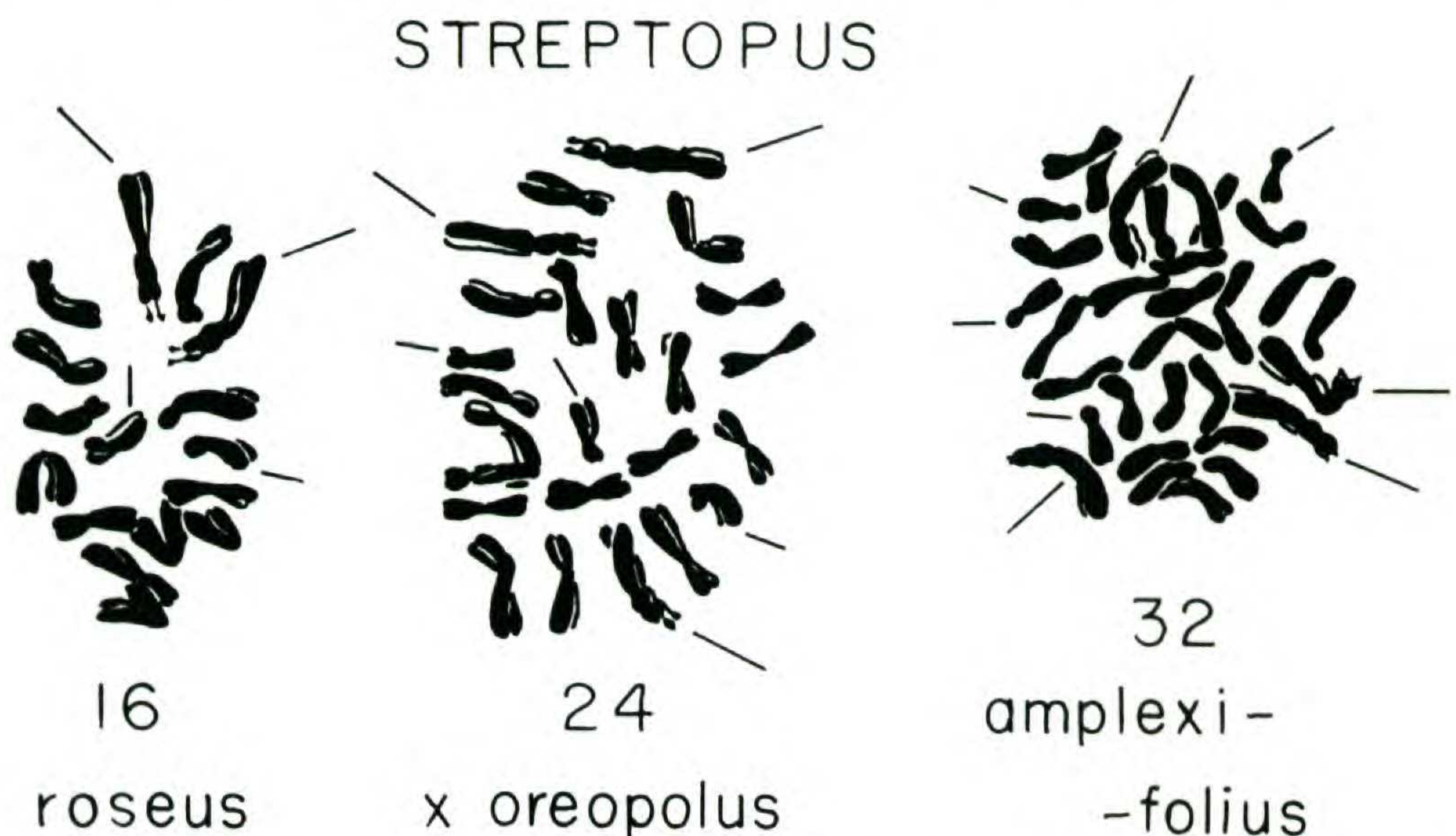


Fig. 1. Chromosomes of *Streptopus roseus*, *S. oreopolus*, and *S. amplexifolius*. In each karyogram the longest and the shortest sets, respectively, are indicated.

triploid ($2n=24$, counted by A. & D. Löve on coll. No. 7512, Lakes of the Clouds, July, 1958), and *S. amplexifolius* is tetraploid ($2n=32$, counted by Dr. S. Kawano on material collected at the Lakes of the Clouds in July, 1960). The chromosomes are large and easily distinguishable. The triploid has distinctly three of each type in its karyogram, as can be seen in Fig. 1, where the smallest and largest chromosomes are indicated. The diploid and tetraploid numbers are in conformity with those previously counted by Therman (1956). The tetraploid number has been counted earlier by Matsuura and Sutô (1935), by Satô (1932), and by Mattick (in Tischler, 1950).

A further study of the plants collected on Mt. Washington showed that the pollen of *S. oreopolus* is completely sterile, whereas that of *S. amplexifolius* and *S. roseus* has 95% or more good pollen grains, when stained with aceto-orcein. In spite of the fact that all fruits collected looked mature and well-filled, the seeds of the *S. oreopolus* fruits proved to be shrivelled and infertile. All available herbarium material of *S. oreopolus* from Newfoundland, the Mingan Archipelago, and the Gaspé Peninsula was checked for these features and it can be stated with certainty that the taxon is sterile everywhere in its range.

The conclusion seems therefore unavoidable that Fernald (1907) was right in his suggestion that *S. oreopolus* might be a hybrid between *S. amplexifolius* and *S. roseus*. It remains to discuss those facts emphasized by Marie-Victorin (1929) and Fassett (1935) which might be considered as negative evidence against such an interpretation of the taxon.

Streptopus oreopolus differs from its two parent taxa by the dark perianth color and by the copiously papillate perianth segments. No explanation for the appearance of these features in the hybrid can be given but the possibility should be considered that the hereditary material of the tetraploid *S. amplexifolius* could contain recessive characters which might become apparent in its hybrid with *S. roseus*.

Neither in the field nor among herbarium material have we seen an intermediate or transitional type between *S. oreopolus* and either *S. amplexifolius* or *S. roseus*. The interpretation of the form observed by Fassett (1935) in the Tuckerman Ravine as a hybrid between *S. amplexifolius* and *S. oreopolus* appears to be incompatible with the observed complete sterility of *S. oreopolus*, and it seems likely that this plant might have been only a somewhat atypical specimen of either *S. oreopolus* or *S. amplexifolius*.

For a sterile hybrid taxon which can spread only by means of its rhizomes, the distribution of *S. oreopolus* is indeed a strange one. Whereas the ranges of the two parent species overlap over a wide area, the distribution of the

hybrid is restricted to a few localities which are distinguished by their wealth of taxa with relict character and highly localized distribution. In these localities, *S. oreopolus* seems generally to be frequent or even common. According to Fernald (1927, p. 76), *S. oreopolus* is an "abundant species of subalpine woods and meadows of the Shickshock Mts. of Gaspé and . . . equally characteristic of subalpine slopes of northwest Newfoundland". On the wide expanse of Tabletop Mt. in the Gaspé, Fernald (1907, p. 106) found it to be "always more abundant than *S. roseus* and *S. amplexifolius*". Stebbins (1929, p. 142) observed *S. oreopolus* on Mt. Katahdin to be: "Abundant on damp slopes above timber line in both the North and South Basins". We ourselves found it on Mt. Washington to be only local in distribution and less frequent than the other two taxa.

It does not appear possible at present to give a well-founded explanation for the distribution of *S. oreopolus*. In the subalpine region of Mt. Washington, *S. amplexifolius* and *S. roseus* were observed by us in many localities growing in large numbers side by side. The flowering seasons of the two species were found also to be largely overlapping. *Streptopus oreopolus* was seen always in the vicinity of the two other taxa except for the occurrence along the Oakes Gulf Trail at 4300' alt. where no *S. roseus* was observed. Similar conditions are indicated for the Shickshock Mts. by Fernald (1907). In agreement with the interpretation of *S. oreopolus* as a hybrid, the suggestion might therefore be made that the range of *S. oreopolus* represents simply areas of maximum possibilities for hybridization between *S. amplexifolius* and *S. roseus*. As an additional factor determining the distribution of *S. oreopolus* the possibility might be considered that the hybrid taxon represents a genotype which is especially well adapted for a subalpine or cool coastal environment.

H4525 KENSINGTON, MONTRÉAL 28.

DEPARTMENT OF BIOLOGY, MOUNT ALLISON UNIVERSITY,
SACKVILLE, N. B.

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LITERATURE CITED

- FASSETT, N. C. 1935. A study of *Streptopus*. *Rhodora* 37: 88-113.
- FERNALD, M. L. 1906. The genus *Streptopus* in Eastern America. *Rhodora* 8: 69-71.
- . 1907. *Streptopus oreopolus* a possible hybrid. *Rhodora* 9: 106-107.
- . 1926. Two summers of botanizing in Newfoundland. *Rhodora* 28: 89-111, 115-129, 161-178.
- . 1927. *Streptopus oreopolus* in the White Mountains. *Rhodora* 29: 76.
- MARIE-VICTORIN, FRÈRE. 1929. Les Liliiflores du Québec. *Contr. Lab. Bot. Univ. de Montréal* 14: 1 - 202.
- MATSUURA, H. and SUTÔ, T. 1935. Contributions to the idiogram study in phanerogamous plants. I. *Journ. Fac. Sci. Hokkaido Imp. Univ.* V, 5: 33-75.
- PEASE, A. S. 1924. Vascular flora of Coös County, New Hampshire. *Proc. Boston Soc. of Nat. Hist.* 37, 3: 39-388.
- SATÔ, D. 1942. Karotype alteration and phylogeny in Liliaceae and allied families. I and II. *Jap. Journ. Bot.* 12: 57-161.
- STEBBINS, G. L. JR. 1929. Some interesting plants from Mt. Katahdin. *Rhodora* 31: 142-143.
- THERMAN, E. 1956. Cytotaxonomy of the tribe Polygonatae. *Amer. Journ. Bot.* 43: 134-142.
- TISCHLER, G. 1950. Die Chromosomenzahlen der Gefäßpflanzen Mitteleuropas. s'Gravenhage.